Ticking time: How does aging affect tympanal organ integrity in female crickets? A descriptive study

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Abstract

The perception of acoustic signals is crucial for mate selection and reproductive success in crickets. While the tympanal organs on the fore tibia play a key role in this process, little is known about how aging affects their structural integrity. This study investigated age-related wear on the tympanal organs of female *Gryllus* (*Gryllus*) *assimilis* (Fabricius, 1775), comparing young and older adults. We hypothesized that structural degradation of the posterior tympanal membrane (PTM) increases with age, potentially impairing auditory perception. To test this, we conducted an ultrastructural analysis of tympanal damage using scanning electron microscopy. Our results describe a deterioration of the PTM, including excrescence, plaque formation, fungal agglomerates, cracks, and perforations. Additionally, a reduction in the integrity of the surrounding sensory hairs was observed. These findings demonstrate that aging significantly affects the PTM structure in female field cricket, which may ultimately compromise the cricket's ability to accurately perceive and respond to acoustic cues. Understanding tympanal wear offers valuable insights into the broader impacts of aging on auditory systems. Future research should explore the relationship between tympanal degradation and reproductive success, as well as investigate cellular-level changes using techniques such as transmission electron microscopy.

Keywords

Acoustic perception, courtship, mechanoreception, posterior tympanal membrane, reproductive behavior, senescence, sensory degradation, sensory organs

Introduction

Acoustic communication is a cornerstone of reproductive behavior in many orthopterans, particularly crickets. Males produce calling songs to attract mates, while females rely on their auditory system to assess and select partners based on acoustic features such as frequency, duration, and pulse rate (Gerhardt and Huber 2002, Bertram and Rook 2012, Schöneich 2020). Crickets have two ears located in the proximal region of the tibia of each foreleg (Schneider et al. 2017, Nishino et al. 2019). Each ear contains two tympanal membranes: the anterior tympanal membrane (ATM), which is smaller and thicker and is considered to play little to no role in sound reception and filtering, and the posterior tympanal membrane (PTM), which is recognized as the main structure responsible for detecting sound (Hill 1974, Paton et al. 1977, Michelsen 1998, Schneider et al. 2017, Nishino et al. 2019, Latham et al. 2024).

Cricket hearing relies on a highly specialized pressure difference receiver mechanism that allows the detection of directional sound cues. These orthopterans achieve directional hearing through their unique tympanal organ structure, which is intricately connected to the acoustic trachea. The tympanal organ of crickets functions as a four-channel system, where sound reaches both the internal walls of the acoustic spiracles (located in the thorax) and the PTM on the same (ipsilateral) and opposite (contralateral) sides of the body (Michelsen 1994, Michelsen and Löhe 1995, Michelsen 1998). The acoustic trachea plays a critical role in directional hearing by transmitting sound waves through multiple pathways, creating pressure differences that enhance auditory sensitivity. Michelsen and Löhe (1995) demonstrated that the acoustic trachea acts as an internal delay line, modifying the phase of sound waves before they reach the tympanal membrane. Rather than functioning as simple pressure receptors, the tympana detect and respond to the difference in pressure between externally and internally transmitted sound waves, enabling precise localization of sound sources.

The sophisticated auditory system allows crickets to distinguish subtle directional variations, and the pressure difference mechanism is finely tuned to the carrier frequency of cricket calls, maximizing the reception of conspecific signals while filtering out background noise. This auditory precision is particularly crucial for mate selection, as female crickets rely on male calling songs to identify and choose suitable mates (Yack 2004). By accurately discerning these acoustic signals, females optimize their reproductive success, reinforcing the importance of maintaining the structural and functional integrity of the tympanal organs. This auditory

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capability plays a key role in sexual selection, as females depend on sound-based cues to assess potential mates (Simmons 1991, Wagner and Reiser 2000, Stumpner and Helversen 2001, Rebar et al. 2009, Bertram and Rook 2012, Shestakov and Vedenina 2015, Botha et al. 2017).

However, like any biological structure, tympanal membranes are not immune to the effects of wear and aging. In a broader biological context, wear is defined as the mechanical degradation of structures due to use and external forces, as seen in the teeth and bones of vertebrates (Britannica 1998, Calandra et al. 2016, Martisius et al. 2018). Among invertebrates, dactyl wear in crustaceans has been used to estimate age (Fonseca and Sainte-Marie 2008). In crickets, while previous studies have shown that older females exhibit reduced discrimination of male calling songs (Prosser et al. 1997), little attention has been given to the potential role of tympanal organ degradation in this decline. Akai and King (1982) reported the structural deterioration of insect auditory organs over time, suggesting that wear could directly affect acoustic perception and phonotactic responses in aging females.

The consequences of early tympanal deterioration extend beyond individual reproductive fitness, potentially disadvantaging individuals that experience premature deterioration. Understanding this process provides insights into the behavior and ecophysiology of orthopterans. Sensory efficiency—primarily the auditory sense—influences not only mate selection and conspecific communication but also predator detection and avoidance, environmental awareness, territorial disputes, and aggression (Yack 2004, Göpfert and Hennig 2016, Yack et al. 2020), shaping survival and reproductive strategies in diverse ecological contexts. Environmental factors such as habitat acoustics, mechanical stress, and age-related physiological changes may exacerbate sensory degradation, affecting population dynamics and behavioral interactions (Arking 1998, Devaraju 2015).

This study investigated the wear of tympanal organs in female *G.* (*G.*) *assimilis* by describing structural changes at macroscopic and ultrastructural levels. Focusing on the PTM, we compared young and older adult females to describe the types and extent of wear and herein discuss its implications for acoustic perception, mate selection, and reproductive success. By addressing these aspects, our research provides a foundation for exploring sensory senescence in orthopterans, contributing to a deeper understanding of the interplay between aging, ecophysiology, and reproductive strategies in acoustically driven insects.

Material and methods

Crickets rearing.—Jamaican field crickets, *G.* (*G.*) *assimilis*, were reared in the Terrestrial Invertebrates Bioterium at the Institute of Biological Sciences, Federal University of Rio Grande (FURG), Rio Grande/RS, Brazil. The crickets were maintained under a controlled light and temperature regime with a 12-hour light: 12-hour dark photoperiod (12hL:12hD) and an ambient temperature of 26 ± 1 °C. From hatching, they were fed *ad libitum* with Golden® commercial cat food. The crickets were kept in plastic boxes (41 × 29 × 13 cm) with egg cartons to provide hiding places. To prevent injuries due to copulation, all nymphs from the 4th stage onwards were sexed and separated by sex prior to the start of the experiments, following a previously established rearing protocol for this cricket species (Limberger 2021a).

Experimental design.—Female crickets from the same cohort were randomly taken from the colony and assigned to two experimental groups. The first group consisted of crickets at normal reproductive age, approximately 15 days after the imaginal molt. The second group consisted of older females, approximately 30 days or more after the imaginal molt. These age groups were selected to represent the early and late stages of adult life, with the 15-day group being at peak reproductive capacity and the 30-day group representing senescent individuals (Limberger et al. 2021a). Data related to life span and egg production for these experimental groups have been previously published and demonstrated biological significance for the female field crickets in the context of aging (see Limberger et al. 2021a, 2022).

Scanning electron microscopy of the PTM.—Female crickets from each age group were cold anesthetized on ice, and the forelegs were carefully removed by disrupting the femur–trochanter joint using a pair of tweezers. The forelegs were used to observe the posterior tympanal membrane (PTM) on the tibia under scanning electron microscopy (SEM). The forelegs were individually dehydrated in an ascending ethanol series (70%, 80%, and 90% for 1 h each), then stored in 100% ethahol and air-dried for 24 hours before examination. The samples were mounted on holders using double-sided carbon tape, sputter-coated with gold (Denton Vacuum Desk V), examined and photographed with a Jeol JSM-6610LV SEM at 10 kV to 15 kV (Limberger et al. 2021b) in the Centro de Microscopia Eletrônica do Sul (CEME-Sul) at the Federal University of Rio Grande (FURG).

Tympanal wear classification.—To characterize the alterations observed in the PTM, five distinct types of wear were defined:

- Excrescence: A rugged protrusion rising above the cuticular surface of the tympanal membrane, forming a visible prominence.
- Plaque formation: Formation of a cuticle-enriched plaque, modifying the natural morphology of the tympanum.
- Fungal agglomerate: Presence of fungal hyphae and spores colonizing the tympanal surface, indicating potential fungal infection or colonization.
- Crack: Cracking between the cuticle of the tympanum and the cuticle of the tibia (at the insertion point), representing structural damage.
- Perforation: Presence of perforations or fissures in the tympanal membrane, indicating more severe damage to the integrity of the PTM.

These wear types were used to classify and compare the morphological changes observed in female crickets of different ages.

Results

During the natural aging process of the PTM in *G.* (*G.*) *assimilis* females, several morphological changes occur, reflecting ontogenetic development. In fifth-instar nymphs, the microtrichia—microscopic mechanoreceptors covering the PTM—are underdeveloped and display a less defined morphology compared to adults (Fig. 1A, B). After the imaginal molt, during adulthood, the tympanal "scar" becomes clearly visible, marking the structural differentiation between the tibial cuticle and the tympanal membrane. At this stage, the microtrichia become more pronounced and spiny, acquiring a thorn-like appearance (Fig. 1A, B).

Comparison of young (15-days-old) and old females (30-days-old) revealed macroscopic differences (Fig. 2A–E). The tympanal

membrane of younger females exhibited a smooth and uniform surface, whereas that of older females showed structural degradation. The most prominent alterations included a marked reduction in the number and integrity of bristles surrounding the tympanum. Additionally, in some cases, localized melanization was observed, suggesting an immune response to injuries on the PTM (Fig. 2E).

A detailed morphological analysis using SEM revealed five distinct types of damage affecting the PTM (detailed in the Methods section): excrescence, defined as protrusions on the tympanal surface (Fig. 3A–C); plaque formation, defined as accumulations of cuticular material altering the natural morphology of the membrane (Fig. 4A–D); fungal colonization, defined as hyphal growth and spore formation on the tympanal area (Fig. 5A, B); crack formation, defined as structural discontinuities at the interface between the tympanum and tibial cuticle (Fig. 5C, D); and perforation, defined as damage exposing internal structures, including taenidial fibers (i.e., helically reinforced cuticular thickenings found in the tracheal system wall that provide structural support to prevent tracheal collapse while maintaining flexibility for gas exchange), sometimes associated with fungal presence (Fig. 6A–D). Occasionally, lesions were also observed in young females, with excrescence being the most common (personal observation).

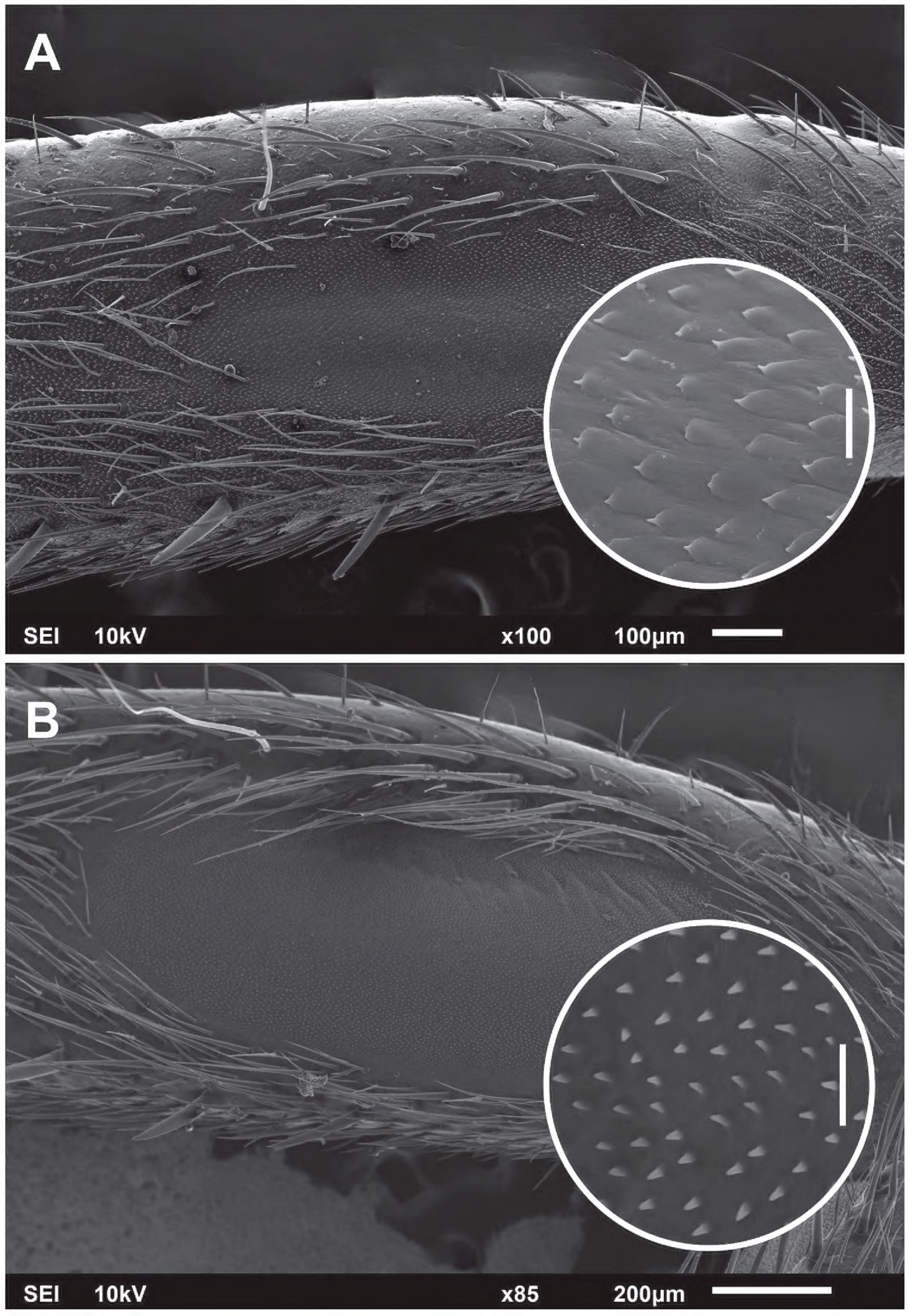

Fig. 1. Ultramorphology of posterior tympanal membrane of *G.* (*G.*) *assimilis* females. **A.** 5th-instar nymph with microtrichia highlighted (circle inset – scale bar: 10 µm). **B.** Early-adult female (14 days) with microtrichia highlighted (circle inset – scale bar: 10 µm).

Discussion

This study is the first to provide a morphological characterization of age-related damage in the auditory organs of cricket females, offering novel insights into the structural integrity of tympanal membranes over time. While crickets have been extensively investigated in the context of bioacoustics (Kostarakos and Hedwig 2012, Pollack and Kim 2013, Hennig et al. 2014, Godthi and Pratap 2015), research has largely overlooked the long-term effects of aging on their auditory structures. Understanding tympanal membrane degradation is crucial, as hearing plays a fundamental role in key behavioral processes such as mate selection and predator avoidance.

The transition from 5th-instar nymphs to adulthood through the imaginal molt is marked by distinct changes in the external morphology of the tympanal membrane, reflecting increased complexity and specialization of its mechanoreceptors (e.g., microtrichia). These modifications likely enhance auditory sensitivity, facilitating the perception of acoustic signals during the reproductive phase. Our findings also revealed that structural damage begins to develop early in adulthood, as observed in females as young as 15 days old, and becomes progressively more pronounced with senescence, particularly after the reproductive period (30–40 days). This highlights the need to consider age-related physiological changes when assessing auditory function and behavior in field crickets and other Orthoptera, as such changes can influence both the reception and production of acoustic signals (Hartley and Stephen 1989). Given that the PTM is the primary structure responsible for capturing sound from the external environment (Kleindienst et al. 1983, Imaizumi and Pollack 1999), its progressive degradation with age may have significant implications for acoustic communication.

Although abiotic factors were carefully controlled during specimen rearing, the lesions observed may be even more severe in natural environments in which individuals are exposed to additional stressors such as predation and adverse climatic conditions. Despite these controlled conditions, we found fungal agglomerates partially or entirely covering the PTM, a phenomenon that appears to be associated with aging. The significant increase in fungal accumulation in older females suggests a decline in grooming behavior over time, as grooming is essential for maintaining the cleanliness of sensory surfaces (Zhukovskaya et al. 2013).

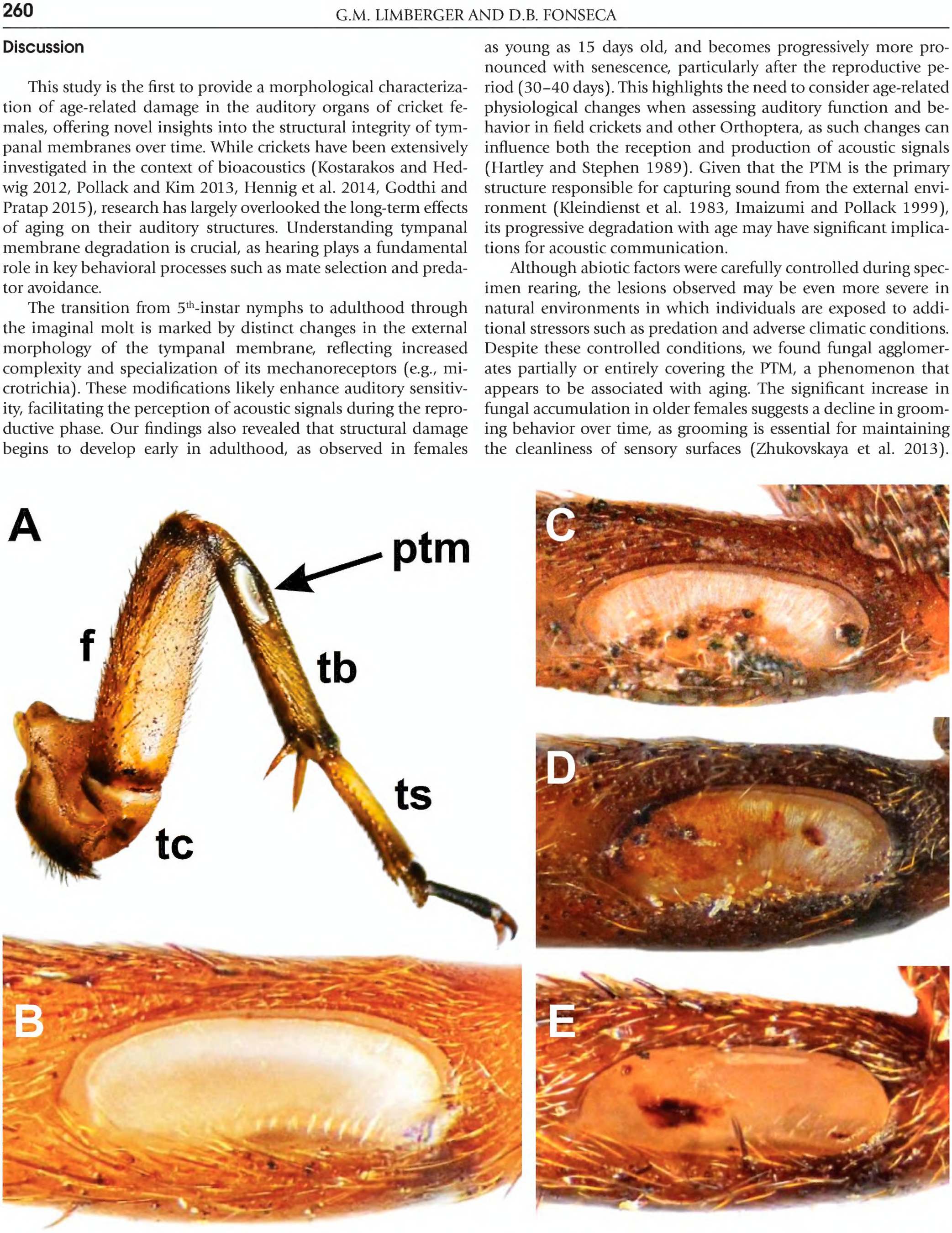

Fig. 2. Images of the posterior tympanal membrane (ptm). **A.** Foreleg anatomy showing key structures: tc – trochanter, f – femur, ptm – posterior tympanal membrane, tb – tibia, ts – tarsus. **B.** Newly molted adult female (15 days). **C, D, E.** Older females (+30 days).

The presence of these fungal masses likely impairs the tympanal membrane's ability to function properly in terms of sound perception. Given that both locomotor activity and grooming naturally decline with age (Scimonelli et al. 1999, Ridgel and Ritzmann 2005), fungal accumulation may be an inevitable consequence of aging exacerbated by the reduced capacity for self-cleaning and immune senescence. In contrast, excrescences, which are superficial lesions, are likely to have a more limited impact on auditory function when occurring in isolation.

Paton et al. (1977) demonstrated that perforations in the PTM, or even its occlusion with Vaseline®, significantly reduce the sensitivity of auditory interneurons by diminishing sensory input. Furthermore, as the size of the perforation increases, the sensitivity threshold of nerve cells in the affected area rises progressively until reaching a critical point, ultimately leading to a loss of tuning. This underscores the crucial role of maintaining the structural integrity of the tympanal membrane (Paton et al. 1977). Due to its irreversible nature and tendency to expand over time, perforation was considered the most severe type of lesion. Beyond its impact on auditory function, it also facilitates the direct entry of pathogens and dust into the insect's body, as hemolymphatic channels and tracheae are located nearby (Friedman 1972, Schneider et al. 2017). A similar concern applies to cracks between the tympanal and tibial cuticles, as the structural continuity between these regions is essential for maintaining auditory sensitivity (Ball and Cowan 1978).

In this study, the occurrence of fungal agglomerates, excrescences, plaques, cracks, and perforations increased with chronological age, characterizing the morphological aging of the PTM and its consequent decline in efficiency. Notably, the peak of tympanal wear appears to occur in middle-aged females, which is particularly relevant, as this period (15 to 30 days post-imaginal molt) coincides with the maximal reproductive activity of this species (e.g., oviposition rate; see Limberger et al. 2021a, 2022). To further understand the implications of these structural changes, comparative studies incorporating behavioral analyses are needed to assess the relationship between tympanal damage and reproductive success in females. Additionally, ultrastructural investigations using transmission electron microscopy could provide valuable insights into cellular and tracheal modifications throughout insect senescence.

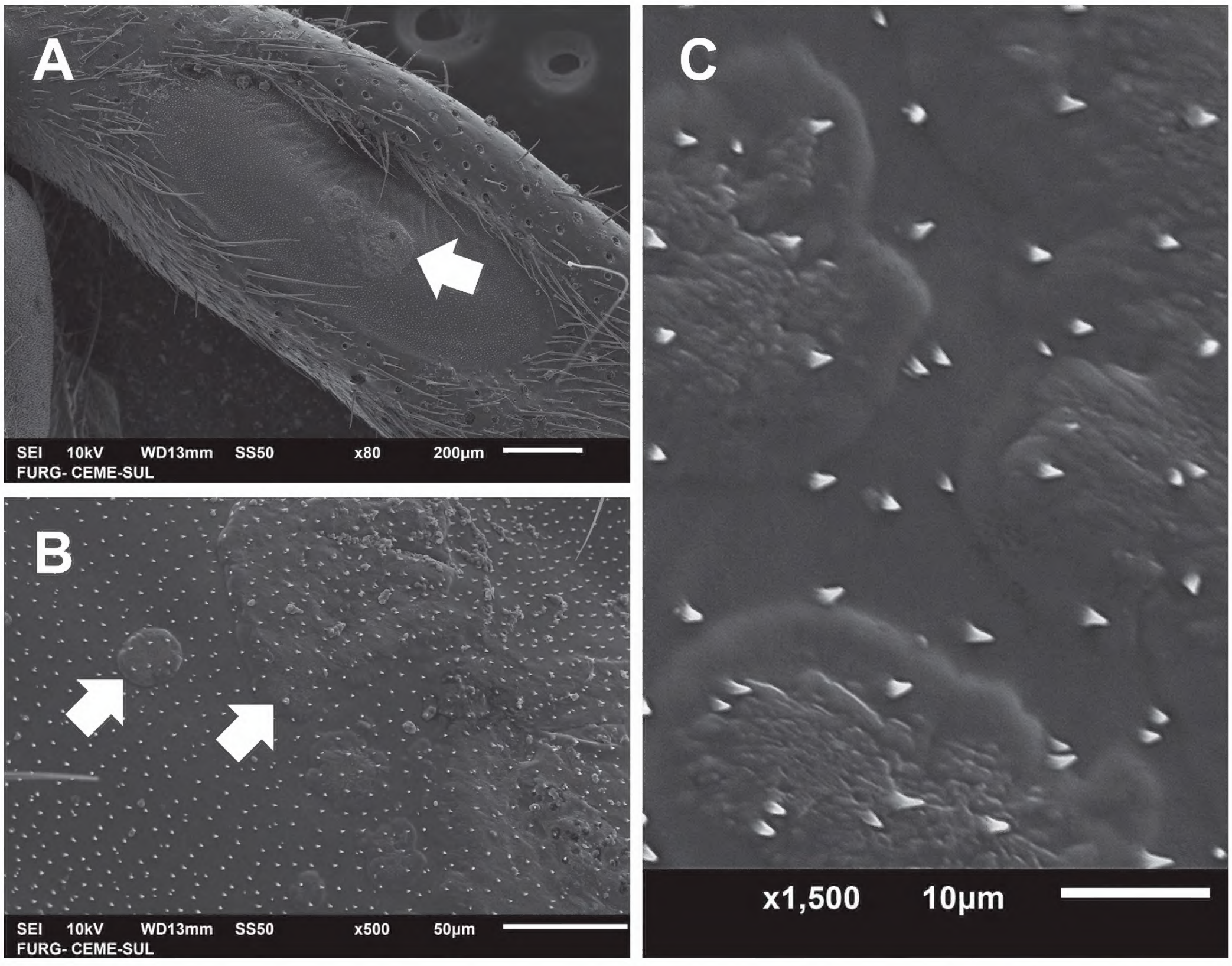

Fig. 3. Excrescence. **A.** Rugged protrusions rising above the cuticle of the tympanal surface, forming prominent bumps on the membrane. Damage observed in the central region of the posterior tympanal membrane (arrow). **B.** Close-up view of the lesion, showing finer details (arrows). **C.** Higher magnification image providing an even closer view of the excrescence and its texture.

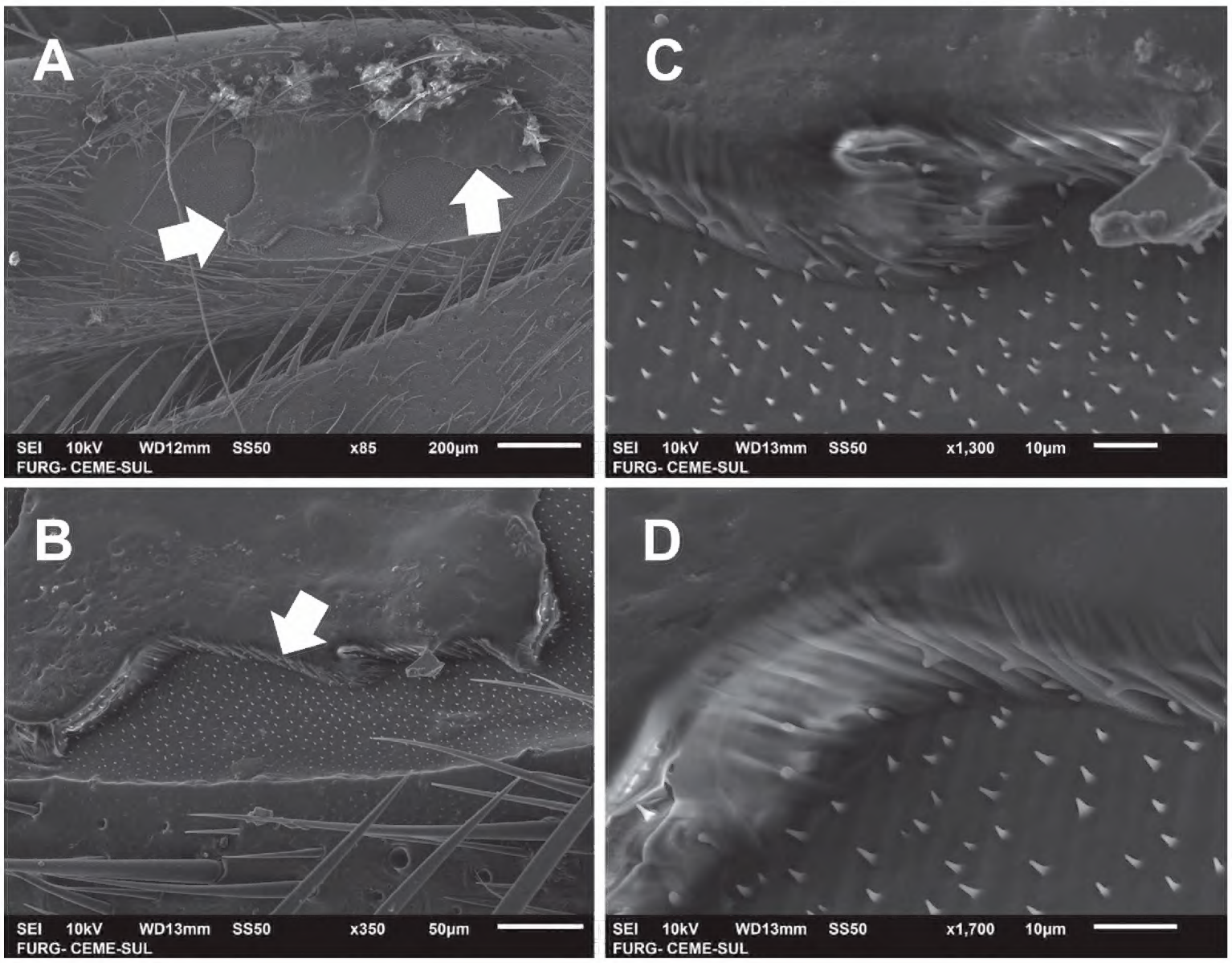

Fig. 4. Plaque formation. **A.** Development of a cuticle-enriched plaque altering the natural morphology of tympanum (arrows). **B.** Close-up view of the plaque formation, highlighting the accumulation of cuticular material (arrow). **C, D.** Higher magnification images providing a detailed view of the plaque's structure and its effect on the tympanal membrane.

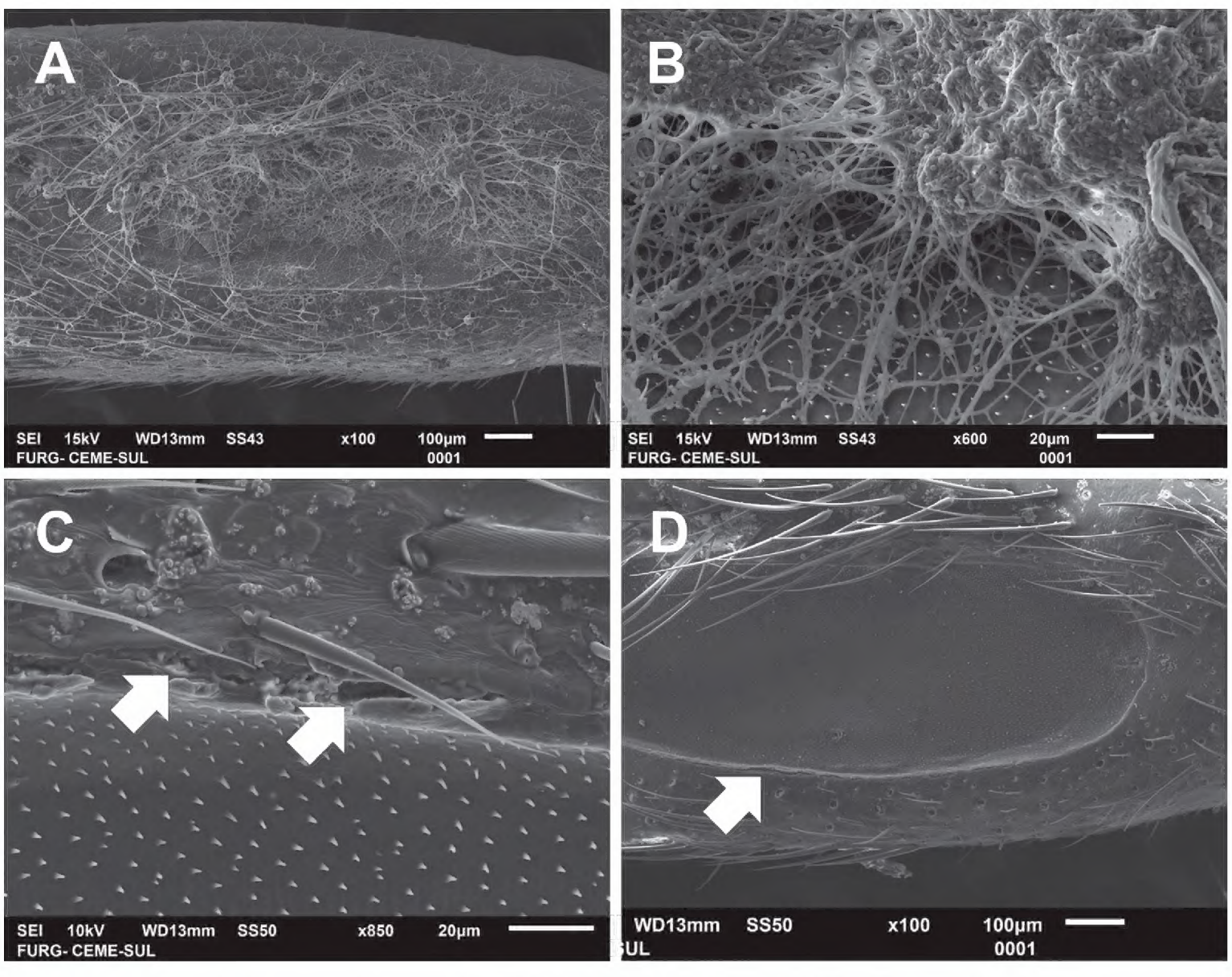

Fig. 5. Fungal agglomerate and crack between tympanal and tibial cuticle. **A.** Fungal hyphae and spores colonizing the external surface of the tympanal membrane. **B.** Close-up view of the fungal colonization, with more detail on the hyphal structure and spore formation. **C, D.** Crack observed at the junction between the tympanal membrane and the tibial cuticle, disrupting the integrity of the interface (arrows).

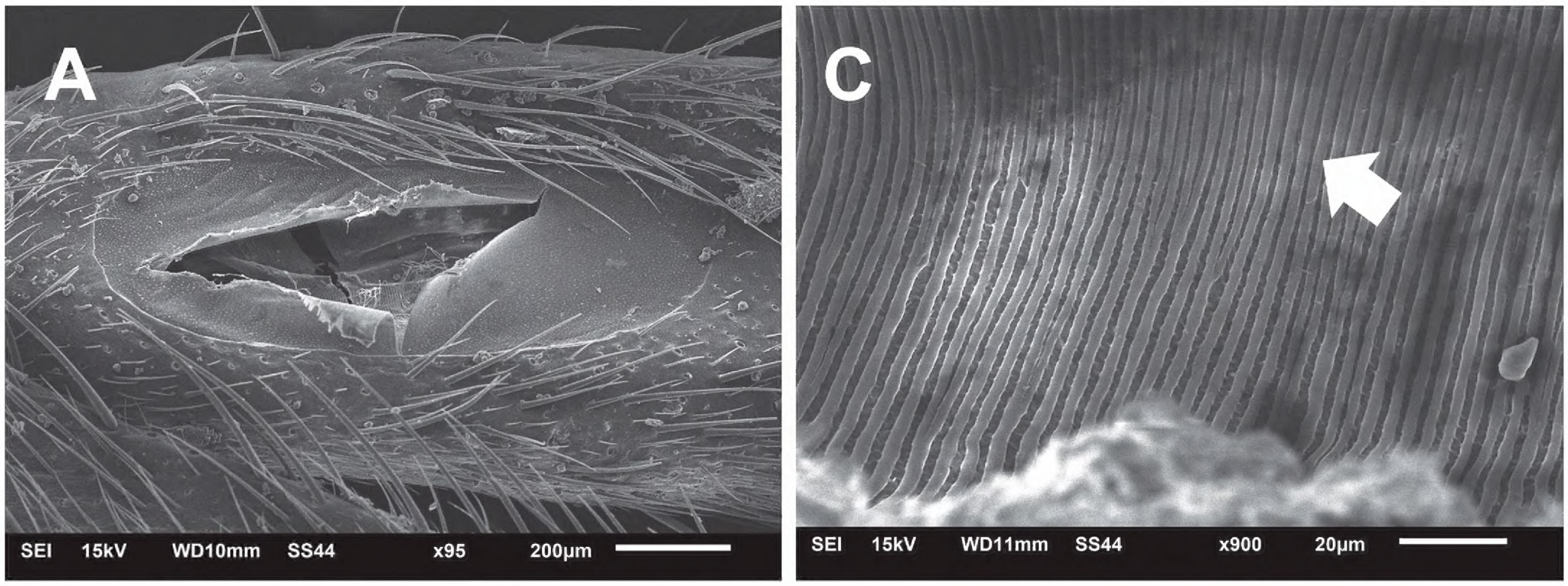

Fig. 6. Perforation. **A.** Large perforation observed in the tympanal membrane, exposing internal structures. **B.** Higher magnification image of the perforation, providing a more detailed view of the damage. **C.** Image showing the taenidial fibers (arrow) forming the acoustic tracheal tube, now exposed due to the perforation. **D.** Fungal colonization observed in the perforated area, with fungal growth on the exposed taenidia (arrow).

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